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Krill demography and large-scale distribution in the southwest Atlantic during January/February 2000

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Abstract

This paper summarizes the results of krill demographic studies from the Commission for the Conservation of Antarctic Marine Living Resources 2000 Survey—a large-scale krill survey across the Scotia Sea conducted in January/February 2000. Standard Rectangular Midwater Trawl net tows were carried out at midnight and midday stations between 20° and 70°W south of the Polar Front. The overall mean numerical density and biomass of krill estimated from nets (247 krill per 1000 m^3 and 18.7 g m^{-2}, respectively) were similar to lower values reported previously for the Southwest Atlantic, and comparable with high values for other regions of the Southern Ocean. Krill varied in mean size across the survey area, with cluster analyses showing three distinct groups of length-frequency distribution. Small juvenile and immature krill occurred east of the South Orkney Islands. Adult krill <50 mm dominated the shelf areas of the Antarctic Peninsula and to the north of the juvenile stock across the Scotia Sea. Adult krill >50 mm were mostly restricted to the west of the South Orkney Islands. Maturity stage composition indicated that peak spawning occurred before early February. Distribution of the spawning stock showed two hotspots, the first between the South Shetland and South Orkney Islands, and the second around the South Sandwich Islands. Reproductive krill were largely absent in the central Scotia Sea and around South Georgia. Krill larvae concentrations occurred slightly to the east of the spawning stock. Mean density of larvae in the western Scotia Sea was 2044 m^{-2}, but only scattered aggregations of larvae were recorded east of 36°W (2 m^{-2}). Recruitment indices for 1- and 2-year-old krill were low in the western part of the survey area, the outflow from the Bellingshausen Sea/Antarctic Peninsula region ($R_1 = 0.0$, $R_2 = 0.11$) indicating spawning failure and/or poor recruitment for several years. In the eastern part of the survey area, mostly the outflow of the Weddell Sea, recruitment indices were high and above the long-term average ($R_1 = 0.60$, $R_2 = 0.72$), suggesting a

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population with constant and successful reproduction, recruitment and mortality. The distribution and structure of the krill population did not show any clear relationship to the position of the major oceanic fronts in the Scotia Sea.
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1. Introduction

The importance of the Scotia Sea as one of the key areas in the circumpolar distribution of Antarctic krill (*Euphausia superba*) has been recognized since the *Discovery* voyages of the early 1920s (Marr, 1962; Mackintosh, 1973). Krill are abundant to the south of 60°S in the western Scotia Sea and the Antarctic Peninsula region, while concentrations in the eastern Scotia Sea extend northward to latitudes of 52°S or less to the north and east of South Georgia. With the rapidly developing krill fishery in the early 1970s, came the need for sufficient quantitative data to enable the development of a management plan, both in relation to the commercial importance of krill and to its importance as a food source for higher predators. In 1981, the first international quasi-synoptic survey (FIBEX; the First International BIOMASS Experiment, El-Sayed, 1994) was undertaken to estimate the krill biomass in the Scotia Sea and to describe the large-scale structure of the stocks. This survey indicated that krill size classes were not uniformly distributed within the Scotia Sea and that mature krill occurred further north than juvenile krill (BIOMASS, 1991). The total krill biomass was estimated at approximately 35 million tonnes (Trathan and Everson, 1994), and this value was subsequently used by the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) to estimate the potential yield of krill and to set precautionary catch limits for the fishery (see references in Hewitt et al., 2004).

Following the FIBEX Survey, research focused on ecological processes and rates, initially through the BIOMASS program (summarized by El-Sayed, 1994) and then through national programs. These resulted in much new information about the krill-based ecosystem (see reviews by Miller and Hampton, 1989; Everson, 2000) but did not include further large-scale acoustic and net sampling surveys. Many of the studies focused on the Antarctic Peninsula and South Georgia areas, with less effort around the South Orkney Islands and almost none in the central Scotia Sea and the region around the South Sandwich Islands. A better understanding of the large-scale coupling between these intensively studied areas has been derived using models (Fach et al., 2002; Fedoulov et al., 1996; Hofmann and Lascara, 2000; Hofmann et al., 1998). However, to date most modeling studies have focused on the fronts and water masses of the Scotia Sea, with few addressing the influence of the Weddell Gyre, which had often been proposed as a separate source of krill in the southwest Atlantic (Everson 1976; Maslennikov and Solyankin, 1980; Melnikov and Spiridonov, 1996; Siegel et al., 1990).

Interannual variation in krill population dynamics is being investigated through a series of long-term standardized mesoscale surveys. These are focused on Elephant Island (the German and US AMLR program, Hewitt and Demer, 2000; Siegel et al., 1998), the western Antarctic Peninsula (the Palmer Long-Term Ecological Research, Ross et al., 1996), and South Georgia (Brierley et al., 1997; Murphy et al., 1998). The results indicate high variability in krill recruitment (Siegel and Loeb, 1995; Watkins, 1999) and large interannual fluctuations in biomass (Brierley et al., 1999; Siegel et al., 1998), and could even indicate an overall decline in krill biomass since 1984 (Siegel et al., 1997).

Concern regarding a possible decline in krill biomass, coupled with uncertainty over the extent to which variability identified during the mesoscale surveys could be applied to the southwest Atlantic krill stock as a whole, were key justifications for the CCAMLR 2000 Survey—a new large-scale survey of krill biomass. Its main purpose has been to generate biomass estimates for setting up-to-date precautionary catch limits for the krill fishery (also see Hewitt et al., 2004). New technology and the use of standardized methods and equipment have been crucial to the provision of more accurate biomass estimates, and thus more reliable catch limits, both for the large scale and for sub-dividing the potential yield into smaller management units. The rationale and design of the CCAMLR 2000 Survey are described by Trathan et al. (2001) and Watkins et al. (2004).

A net sampling program for krill and zooplankton formed the core of the CCAMLR 2000 Survey and had three primary objectives:

- to identify acoustic targets, confirming which targets could be considered as krill, and to obtain krill length-frequency data for target strength estimation;
- to describe krill demography and large-scale distribution patterns of size groups and maturity stages, plus regional recruitment indices and reproductive success during the current spawning season; and
- to describe the zooplankton community structure (see Ward et al., 2004) and the occurrence of major zooplankton taxa such as salps (see Kawaguchi et al., 2004).

This paper reports aspects of the krill population structure, density estimates from net samples, recruitment success and the quasi-synoptic large-scale distribution patterns of size groups, including the spawning stock and krill larvae, to enable a general assessment of the krill populations in the southwest Atlantic.

2. Material and methods

Four vessels participated in the CCAMLR 2000 Survey: the R.V. *Kaiyo Maru* (Japan), the R.V. *Atlantida* (Russia), the R.R.S. *James Clark Ross* (UK) and the *Yuzhmorgeologiya* (USA). Each vessel undertook standard hydro-acoustic measurements along parallel transects across the Scotia Sea between 20° and 70°W. A minimum of two net sampling stations were conducted by each vessel every day (Fig. 1).

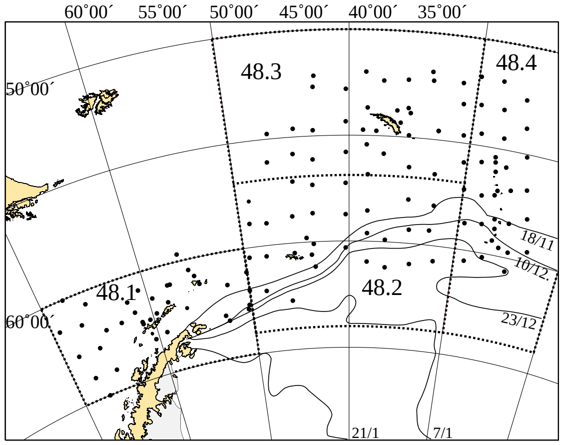

Fig. 1. RMT stations during the CCAMLR 2000 Survey: Subarea 48.1, Antarctic Peninsula; 48.2, South Orkney Islands; 48.3, South Georgia; 48.4, South Sandwich Islands. The northern limit of the ice edge is shown between 18 November 1999 and 21 January 2000 (*source*: www.natice.noaa.gov/pub/Antarctica/).

2.1. Standard gear

All participants used RMT1 + 8 nets (Rectangular Midwater Trawl, Baker et al., 1973). Each net had a flowmeter to estimate the filtered water volume and a real-time time-depth-recorder (TDR) to record the track of the net.

Each day net tows were undertaken in darkness around local midnight and around midday unless directed fishing for acoustic targets had occurred earlier in the day. A quantitative standard double oblique tow was conducted from the surface to 200 m (or to within 10 m of the bottom at stations shallower than 200 m). This depth range was considered the best compromise between time available for sampling and the likely vertical depth range of krill. During the hauls ship speed was maintained at 2.5 ± 0.5 kn and the towing cable was veered at 0.7–0.8 m s^{-1} (42–48 m min^{-1}) and hauled at 0.3 m s^{-1} (18 m min^{-1}). Following Pommeranz et al. (1982) the mouth angle during hauling, and hence the mouth area of the sampling net, was assumed to remain constant at these speeds. The winch was stopped for 30 s once the net reached maximum depth to allow the net to stabilize before retrieval. Deployment times varied from 15 to 45 min.

Directed net sampling also was undertaken during daylight hours to identify selected acoustic targets or scattering layers. However, as these hauls were non-randomly distributed, the results are not included here.

2.2. Laboratory sampling

Samples from the RMT8 were processed for krill and salps while samples from the RMT1 were preserved in a 10% buffered formalin solution for later analysis of zooplankton abundance. Details of the salp analyses can be found in Kawaguchi et al. (2004) and the zooplankton analyses in Ward et al. (2004). This paper focuses on krill. RMT8 samples ranged in weight from a few grams to several kilograms. The total volume of the net catch was measured as total drained sample volume. All the krill were counted in samples of less than 1 l and a sub-sample measured immediately after capture.

Samples greater than 1 l were sub-sampled volumetrically, with the exact protocol depending on the composition of the catch. If the sample mainly comprised krill, then the total drained sample volume was recorded and a quantitative sub-sample was taken randomly and the krill counted. If the sample mainly comprised salps, then the total drained sample volume was recorded, and then all krill were removed from the total sample, counted and measured. Total catch and sub-sample volume and information on fishing depth and filtered water volume were used to generate krill densities and length-density data (m^{-2} or $1000\,m^{-3}$). Protocols for RMT1 ($1\,m^2$ mouth area and 335 μm mesh size) sample analyses from which larval krill abundance was determined are given by Ward et al. (2004).

2.3. Length measurements and maturity staging

The standard krill length measurement was total length; from the anterior margin of the eye to the tip of the telson without the terminal spines. Length-frequency distribution was based on 1-mm increments. On each ship measurements were undertaken by a single person to minimize observer variation (see Watkins et al., 1985). All krill were measured and staged in samples that contained less than 150 krill. For larger catches a minimum of 100 krill were measured and staged. Krill sex and maturity stages were identified using the classification of Makarov and Denys (1981). The maturation index (Loeb et al., 1997; Siegel and Loeb, 1995) was calculated from the proportion of advanced gravid stages (F3C, F3D and F3E) in the female adult population in January 2000.

2.4. Data recording and analysis

Station data and krill counts and measurements were recorded in EXCEL® spread sheets. Krill numerical density was calculated using a simple arithmetic mean, or the software TRAWLCI (described by de la Mare, 1994b). The latter is the standard method used by CCAMLR to estimate densities from trawl samples. The TRAWLCI software was developed for calculating asymptotic confidence intervals for estimates of abundance obtained from standardized net surveys using likelihood ratios from Aitchison's delta distribution. Analyses by de la Mare (1994b) show the abundance estimates appear to be unbiased. However, the number of data points with no krill has a large effect on the precision of the estimates of the parameters of the lognormal component of the delta distribution. Thus, in cases where few hauls contain krill the coefficient of variation (CV) is high and the confidence limits are less reliable. During the CCAMLR 2000 Survey most samples contained krill.

Data analyses were undertaken using the Statistica® software. Following the procedure for the FIBEX Survey (BIOMASS, 1991), cluster analyses of length composition by haul were undertaken to describe similarities between length-frequency distributions and to investigate spatial structure in the krill population. The clustering was based on a similarity matrix derived from Euclidean distances. Stations with a minimum of 20 measured specimens were used to avoid random fluctuations caused by stations with few length groups. Of the 135 net sampling stations 66 were used to derive the similarity matrix. The hierarchical fusion of clusters, and thus the geographical distribution of the various clusters and the related composite length-frequency distributions, was determined by the Complete Linkage method.

Krill recruitment was estimated using length-density data from routine trawls and the CMIX method described by de la Mare (1994a). From the oblique net hauls proportions of recruits were calculated for ages 1 and 2 (R_1 and R_2). The densities of krill in 1 mm length classes were estimated using the measured filtered volume for each haul. A mixture distribution was fitted to these data by maximum likelihood to estimate the proportion of recruits.

3. Results

3.1. Distribution, abundance and biomass

Krill density distribution within the Scotia Sea was highly heterogeneous. Highest densities occurred to the southeast of South Georgia, close to the southern part of the South Sandwich Islands, on the northern shelf of the South Orkney Islands, and near Elephant Island and Livingston Island (Fig. 2). Relatively low densities occurred in the central Scotia Sea and in the northeastern Drake Passage/Antarctic Peninsula area. Krill were mostly absent from the northernmost stations, especially those from the northwestern Scotia Sea, and from the southwestern Drake Passage and stations within the Weddell Sea outflow.

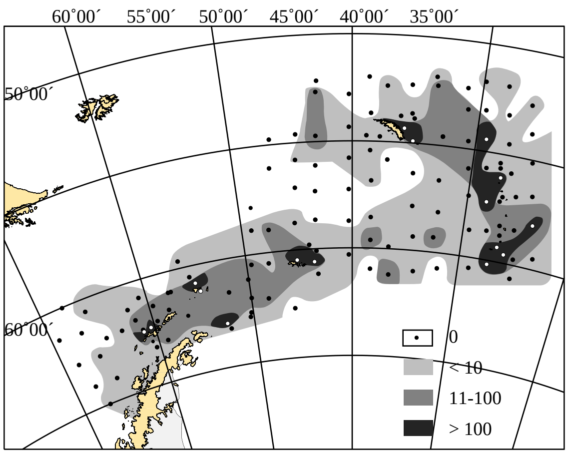

Fig. 2. Krill density (individuals per 1000 m^3) during January/February 2000.

The distribution of krill biomass was similar to the krill density distribution, with the exception of the area to the south of the South Sandwich Islands. In this region, numerical density was high, but biomass moderate, due to a high abundance of small krill.

Tables 1 and 2 summarize the numerical and biomass densities for the survey area as a whole, as well as for the various statistical subareas and the survey strata. As the northernmost stations with zero catch rates are assumed to occur beyond the krill distribution range data for these stations are excluded from the calculation of mean densities within the distribution range of krill (Table 1, stations shown to the north of the shaded area <10 in Fig. 2). The overall mean numerical density within the krill distribution area was 247 krill per 1000 m^3 (Table 1), with a mean biomass of 18.7 g m^{-2} (Table 2). Numerical and biomass densities in the South Orkney area (Subarea 48.2) and around the South Sandwich Islands (Subarea 48.4) are substantially higher than in the Antarctic Peninsula and South Georgia regions. Also, krill densities appear three times higher in shelf areas than in the open ocean (Table 1).

3.2. Length frequencies

Three major clusters were identified (Fig. 3). Cluster 1 (C1) primarily comprised krill <35 mm in length with a single mode at 26 mm (Fig. 4A). The majority of these krill were juveniles (79%) with a few immature animals. The skewed unimodal length-frequency distribution of cluster 3 (C3) was represented primarily by large mature krill (82%) with a mode at 52 mm, such krill are likely to be four or more years old (Siegel, 1987; Wang et al., 1995). There was a higher frequency of intermediate size classes (30–40 mm) in cluster 2 (C2) and a modal size (48-mm) that was slightly smaller than in C3. In all, 55% of krill in C2 were immature and 39% mature. The 48-mm size mode probably represents four-year-old krill, while size

Table 1
Numerical densities

	Average density				TRAWLCI method	
	All samples		Excluding zero catches		Density within distribution range	
	N 1000 m^{-3}	S_E	N 1000 m^{-3}	S_E	N 1000 m^{-3}	S_E
Survey strata						
Antarctic Peninsula	44.8	25.4	58.8	32.8	90.3	68.2
Scotia Sea	53.8	35.2	77.9	50.6	38.3	23.4
South Sandwich Islands	268.9	106.8	308.8	121.0	754.3	615.1
All strata	124.2	35.9	158.9	45.4	247.5	136.4
CCAMLR subareas						
Subarea 48.1	37.2	17.0	45.8	20.7	64.4	39.6
Subarea 48.2	134.0	94.3	201.0	139.3	127.3	113.1
Subarea 48.3	74.8	50.2	101.5	67.7	75.4	52.9
Subarea 48.4	268.9	106.8	308.8	121.0	754.3	615.1
Bathymetric zone						
Oceanic region	89.5	37.0	120.7	49.4	153.3	91.0
Shelf areas	236.2	102.7	256.7	110.8	487.1	379.1

Note: Average densities were calculated as a simple arithmetic mean and by applying the TRAWLCI method according to de la Mare (1994b). Antarctic Peninsula (50–70°W), Scotia Sea (30–50°W) and South Sandwich Islands (20–30°W). Oceanic regions are defined as areas >1000 m, shelf regions are defined as areas <1000 m.

Table 2
Krill biomass densities within the distribution range (excluding zero catches) from routine RMT net samples

	Mean biomass density			
	Arithmetic mean		TRAWLCI method	
	g m^{-2}	S_E	g m^{-2}	S_E
Survey strata				
Antarctic Peninsula	10.3	5.7	12.0	8.2
Scotia sea	6.2	4.0	3.6	2.1
South Sandwich Islands	20.2	12.1	27.3	20.3
All strata	14.0	5.0	18.7	9.4
CCAMLR subarea				
Subarea 48.1	8.0	3.6	10.0	5.7
Subarea 48.2	29.3	23.8	13.6	11.9
Subarea 48.3	7.0	5.1	6.0	4.1
Subarea 48.4	20.2	12.1	27.3	20.3
Bathymetric zone				
Oceanic region	10.4	5.2	10.6	5.8
Shelf areas	25.7	13.5	47.9	35.5

Note: Biomass densities were calculated as a simple arithmetic mean and by applying the TRAWLCI method according to de la Mare (1994b). Antarctic Peninsula (50–70°W), Scotia Sea (30–50°W) and South Sandwich Islands (20–30°W). Oceanic regions are defined as areas >1000 m, shelf regions are defined as areas <1000 m.

classes of 30–45 mm usually represent 2- and 3-year-old krill; the frequency of these size/age groups was relatively low in C2.

A spatial succession of length and maturity stages (Fig. 5) is typical for the area along the Antarctic Peninsula, and also has been described for the Scotia Sea (BIOMASS, 1991; Siegel, 1988). In summer 2000, the small, juvenile and immature krill represented by C1 occurred mainly along the western side of the South Sandwich Islands northward to the southeastern shelf of South Georgia. This cluster and the related krill size classes did not occur in the western survey area, where they usually occur on the shelf of the Antarctic Peninsula. C3, with the largest mature krill, occurred in a continuous band across the western oceanic waters of Drake Passage, and to the north of the South Shetland and South Orkney Islands. A few scattered stations to the east of the South Sandwich Islands also belonged to C3. However, the relevant size groups of this cluster were missing from the central Scotia Sea. The relatively large intermediate krill of C2 formed a continuous band across the Scotia Sea, extending from south of C3 in the Bransfield Strait to the

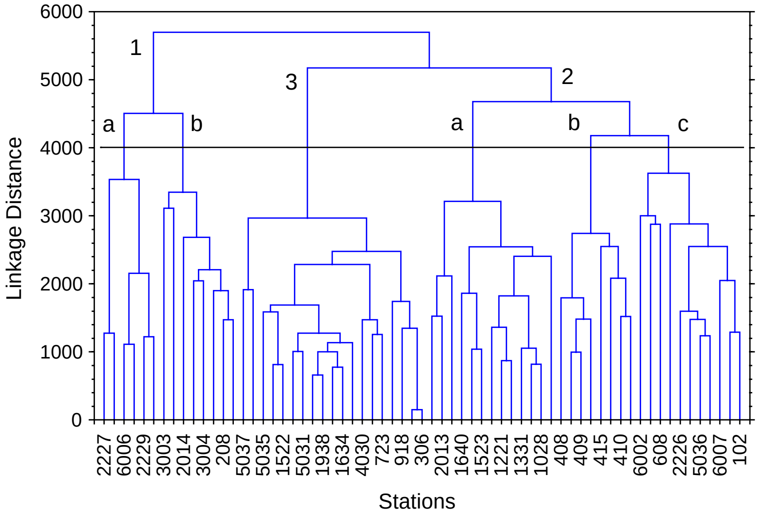

Fig. 3. Dendrogram of the cluster analysis based on relative frequency of krill size groups.

north of South Georgia and to the east of C1 and the South Sandwich Islands.

The composite length-frequency distributions for C1, C2 and C3 provide an approximate picture of the spatial structure of the Scotia Sea krill population, although length-frequency distributions within clusters were not uniform. Fig. 3 shows two sub-groups in C1 (C1a and C1b) and three sub-groups in C2 (C2a, C2b and C2c). The degree of variability in length frequencies within each cluster is demonstrated in Fig. 4, which shows the size composition of krill for the relevant sub-groups.

C1a contains six stations with high krill densities that dominate the overall length-frequency distribution of C1 with a modal size of 28 mm (Fig. 4A). The unimodal length-frequency distribution of C1b had a slightly larger mode of 31 mm. However, the eight stations with this size composition had relatively low densities such that they contributed very little to the overall length frequency of C1. The smaller krill in C1a covered stations in the southeastern corner of C1, whereas the slightly bigger krill in C1b occurred in the southwestern corner of C1 and to the southeast of South Georgia. However, there was no clear latitudinal effect that could be interpreted as a continuous change in size or growth from south to north.

C2 is more variable than C1 and is sub-divided into three sub-groups. The length frequency of C2a is similar to the overall composite length-frequency distribution of C2 with a strong mode at 48 mm (Fig. 4B). Size classes <43 mm are hardly present in C2a length frequencies. Stations belonging to this sub-group mainly occur along the Antarctic Peninsula, with a few scattered stations around South Georgia and the South Sandwich Islands. Length frequencies for C2b and C2c show no mode at 48 mm but have the majority of krill covering a broad distribution of sizes between 30 and 45 mm, with a slightly higher proportion of bigger size classes in C2b. In general, these length-frequency distributions represent the left shoulder of the composite length-frequency distribution of C2. Stations with medium-sized krill and belonging to C2b and C2c occurred to the east of the South Orkney Islands, north of South Georgia and around the South Sandwich Islands.

Krill densities also were substantially different in different parts of the South Atlantic; highest densities occurred in the eastern stratum, with much lower densities to the west of the South Orkney Islands. These regional density differences have a strong effect when standardizing length frequencies to set up a composite length-frequency distribution for the krill stock in the Southwest

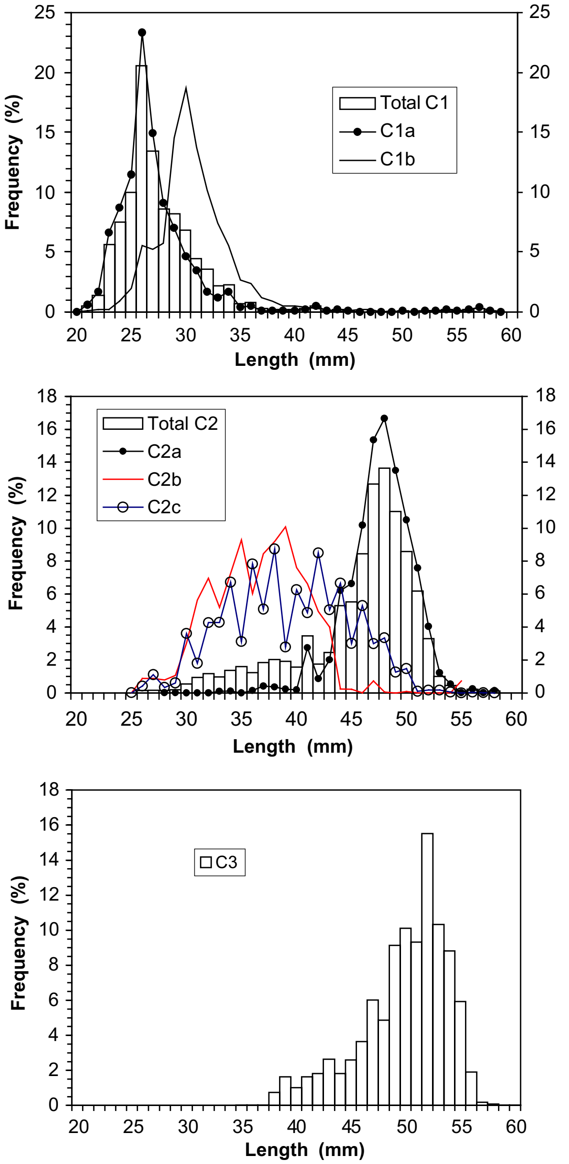

Fig. 4. Krill length-frequency distributions for geographical clusters C1, C2 and C3.

Atlantic as a whole (Fig. 6). The krill stock(s) of the survey area were clearly dominated by the presence of small krill with a mode of 26 mm, although these occurred only in parts of the eastern sector. The second mode at around 48 mm also showed the strong influence of the relatively high densities in parts of C2.

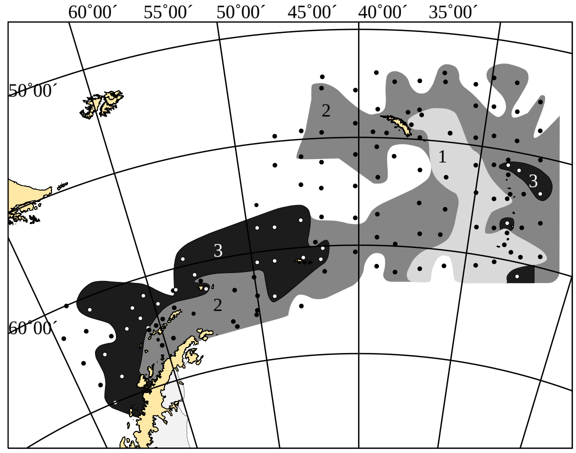

Fig. 5. Spatial distribution of krill size clusters in January/February 2000.

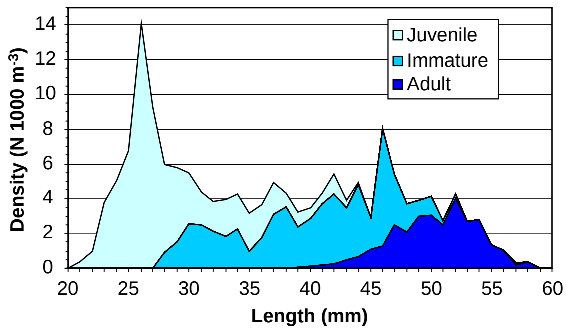

Fig. 6. Composite length-density distribution (individuals per 1000 m^3) for the developmental stages.

3.3. Maturity stage composition

Fig. 6 shows that the small size group consisted exclusively of one-year-old juvenile krill. Note, however, that a second mode of juvenile krill occurred at 35 mm, which suggests that such krill may be two years old based on the length-at-age data from Siegel (1987) and Pakhomov (1995) where the January mean length-at-age for two-year-old krill was usually 36 mm. In January 2000, immature stages reached a maximum of >50 mm, although the mean expected length-at-maturity for males is 42 mm (Siegel and Loeb, 1994), and for females is even smaller. Adult krill were mostly >48 mm.

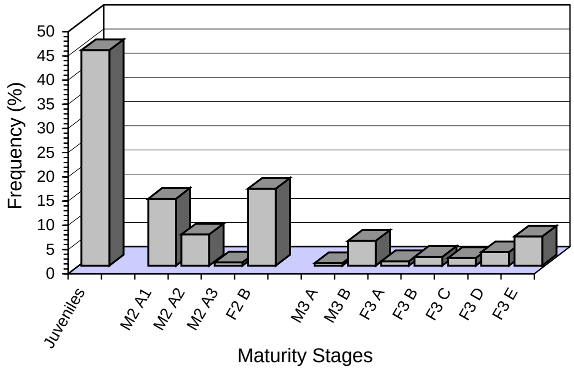

Fig. 7. Overall krill maturity stage composition: M2, immature males; M3, adult males; F2, immature females; F3, adult females; single maturity stages are given according to the classification of Makarov and Denys (1981).

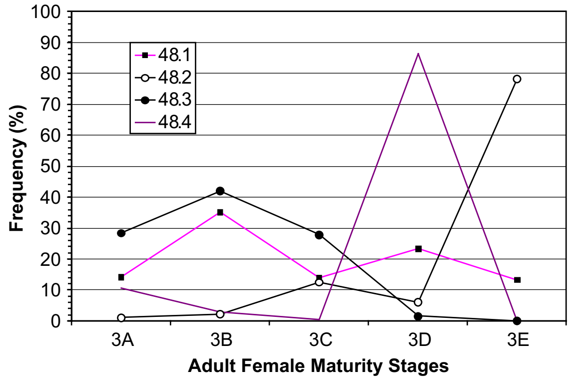

Fig. 8. Development of adult female maturity stages during the spawning season (end January/beginning February 2000): 3A, pre-spawning; 3B and 3C, developing; 3D, gravid; 3E, spent females.

The relative frequency of the various maturity stages shown in Fig. 7. Nearly 45% of the stock was juveniles while >30% were sub-adults (immature stages M2 and F2). Adult female stages, although accounting for <15% of the total stock occurred with increasing frequency as maturity stage progressed from early (F3A) to gravid (F3D) to spent (F3E) stages. More than 6% (almost half the adult females) of the total stock was spent females between the end of January to early February (Figs. 7 and 8).

The maturity index is based on the data shown in Fig. 8 and calculates the proportion of sexually advanced female maturity stages in January (stages 3C–3E) from the total number of adult female stages (3A–3E). A high index indicates an early spawning season (Siegel and Loeb, 1995). For the CCAMLR 2000 Survey the overall index (G) was 0.79, but was comparatively low for the South Georgia region (Subarea 48.3, $G = 0.30$). This reflects the low frequency of gravid (3D) and spent (3E) stages in the South Georgia area, indicating a retarded maturation process. In contrast, high indices indicate maturation was well advanced in the South Orkney Island (Subarea 48.2, $G = 0.87$) and South Sandwich Island (Subarea 48.3, $G = 0.97$) areas, with highest frequencies for spent (3E) and gravid (3D) stages, respectively.

The cluster analysis has shown geographical differences in krill length composition. Since

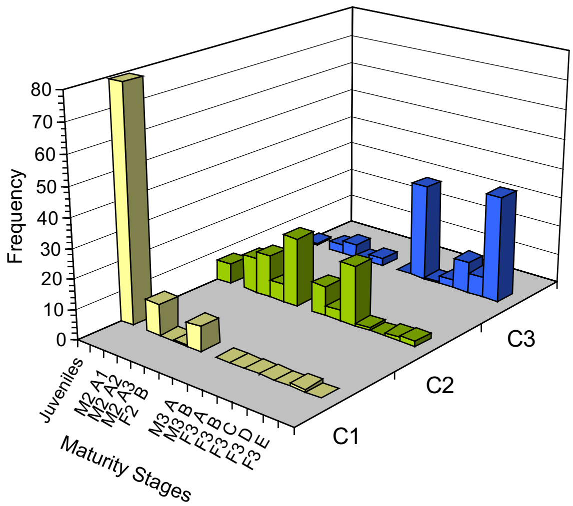

Fig. 9. Krill maturity stage composition for C1, C2 and C3: M2, immature males; M3, adult males; F2, immature females; F3, adult females; single maturity stages are given according to the classification of Makarov and Denys (1981).

length and maturity are closely related, a similar pattern in the spatial distribution of maturity stages is not surprising (Fig. 9). The relative frequency of juvenile krill reached a maximum in C1 (80%); where adult stages contributed only 1% to the krill stock to the southeast of South Georgia. Immature and early pre-spawning adult stages dominated C2 (85%), which covered the

Bransfield Strait and its eastern outflow into the Scotia Sea, as well as the regions north of South Georgia and part of the South Sandwich Island area. The most advanced adult maturity stages occurred in C3 in samples from the northwestern Scotia Sea and off the Antarctic Peninsula. C3 is clearly the spawning stock; more than 85% of krill in this area were reproductively active, i.e. female gravid stages immediately pre- and post-spawning and adult males with empty spermatophore ducts indicative of recent spawning.

The distribution of the spawning stock across the Scotia Sea was not uniform. Two hotspots can be identified from the occurrence of gravid/spent krill (Fig. 10). The first concentration of spawning krill formed a narrow band from the northern side of the South Shetland Islands to just north of the South Orkney Islands. The mean concentration of gravid/spent females was >12 per 1000 m^3 (Table 3). The second spawning concentration occurred in the central and southeastern part of the South Sandwich Islands. The density of spawning krill in the eastern Scotia Sea was much lower. Fig. 10 indicates a lack of krill spawning activity in the central Scotia Sea, around South Georgia and north of the South Sandwich Islands.

The occurrence of spent female stages could be expected to indicate that krill larvae were already present in the water column. Analysis of the RMT1 samples shows that $>40\%$ of the larvae were in calyptopis 1 stage, 32% in calyptopis 2 stage and $<10\%$ accounted for furcilia stages F1–F3. Fig. 11 shows clear differences in larval distribution between different strata of the survey area. The highest concentration of larvae occurred in the western sector, i.e. the central Scotia Sea between Elephant Island, east of the South Orkneys, and southwest of South Georgia.

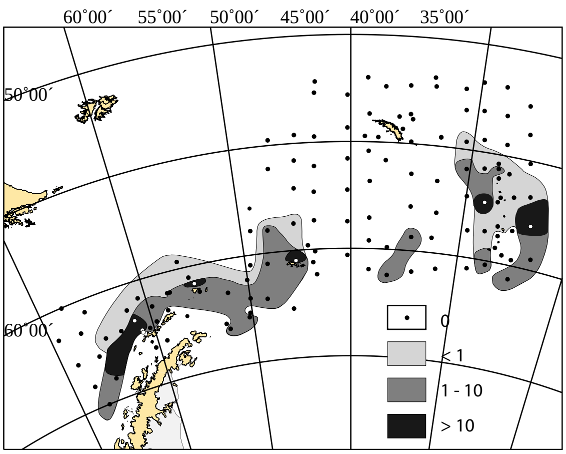

Fig. 10. Geographical distribution of gravid/spent female krill in January/February 2000.

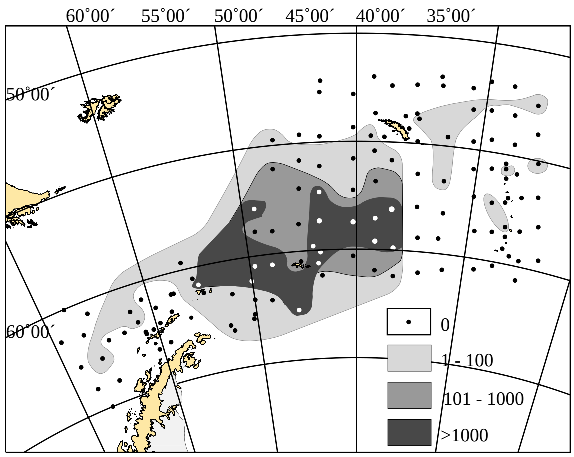

Fig. 11. Geographical distribution of larval krill in January/February 2000.

Table 3
Numerical densities for gravid and spent female krill; average density is a simple mean, densities from the 'TRAWLCI method' are calculated according to de la Mare (1994b)

Area	Average density		TRAWLCI method	
	N 1000 m^{-3}	S_E	N 1000 m^{-3}	S_E
Western Scotia Sea (45°–70°W)	24.9	18.50	12.4	7.07
Central Scotia Sea (30°–45°W)	0.2	0.08	0.2	0.14
Eastern Scotia Sea (east of 30°W)	7.1	5.12	3.8	2.56

Table 4
Density of krill larvae during the CCAMLR 2000 Survey and the FIBEX Survey in 1981

	CCAMLR 2000		FIBEX 1981	
	$N\,m^{-2}$	S_E	$N\,m^{-2}$	S_E
Calyptopis (west)	1841.7	674.7	19,307.9	9357.3
Calyptopis (east)	2.2	0.9		
Furcilia (west)	202.6	109.2	435.2	222.2
Furcilia (east)	0.2	0.1		
Total larvae (west)	2044.3	749.3	18,601.8	8322.6
Total larvae (east)	2.4	1.0		

Note: 'west', west of 36°W; 'east', east of 36°W.

Although there were some scattered stations with records of calyptopis larvae in the South Sandwich Islands region, a sharp boundary occurred around 36°W where larval distribution rapidly stopped. RMT1 samples yielded a maximum of 36,000 krill larvae per m^2 in the western Scotia Sea, but only $25\,m^{-2}$ to the east of 36°W. Table 4 summarizes average larvae densities and emphasizes the difference between the western and eastern Scotia Sea. The western areas along the Antarctic Peninsula also showed relatively low larval densities.

3.4. Age structure and recruitment

Estimates of krill recruitment obtained by applying the method described by de la Mare (1994b) to the length-density distributions are summarized in Table 5. Remarkably, no one-year-old krill recruits (R_1) were observed in the Antarctic Peninsula region (Subarea 48.1) and krill recruitment was relatively low in the South Orkney Islands and South Georgia regions, with slightly more than 4% and 6% of the stock comprising age group 1 + krill. Those one-year olds found in the latter two subareas had come from the eastern section of the subareas; the area west of 45°W showed a complete absence of this krill age-class.

Recruits were found exclusively east of 45°W, with the highest proportion in the South Sandwich Island area, where they dominated the stock. The large number of krill in the eastern part of the survey area also strongly influenced the overall index for the survey area as a whole. An R_1 value of 0.568 is relatively high compared to recruitment values from earlier studies (Siegel and Nicol, 2000). At least in the eastern sector of the South Atlantic the 1998/1999 year class seemed very successful. R_2 values in Table 5 indicate that recruitment of the two-year-old krill in the Antarctic Peninsula area also was poor, with at least two weak year classes in a row in the western Scotia Sea, while krill in the east again showed a recruitment success far above the average recruitment found in the Elephant Island data set (Siegel et al., 2002).

These spatial differences in year-class success had a significant effect on the age structure of the stocks in the different parts of the South Atlantic (Table 6). In the western Scotia Sea, the stock was clearly dominated by relatively old, large and adult krill (also see Sections 3.2 and 3.3). During the preceding years, failure of reproduction and/or poor recruitment had inverted the population

Table 5
Proportional recruitment indices R_1 and R_2 (one- and two-year olds, respectively) from krill length-density distributions; indices calculated according to de la Mare (1994a)

Area	R_1	S_E	R_2	S_E
CCAMLR subarea				
Subarea 48.1	0	—	0.0810	0.1975
Subarea 48.2	0.0430	0.1258	0.2953	0.5300
Subarea 48.3	0.0660	0.0452	0.9212	0.1725
Subarea 48.4	0.7198	0.1738	0.5632	0.2576
Geographic region				
West of 45°W	0	—	0.1110	0.0635
East of 45°W	0.6017	0.2663	0.7280	0.1858
Southwest Atlantic total	0.5680	0.2265	0.4945	0.2006

Table 6
Percentage frequency of age groups in the South Atlantic krill stocks in January/February 2000

Age group	West of 45°W	East of 45°W
1	0	60
2	10	26
3	20	12
⩾4	70	2

pyramid. The eastern Scotia Sea was inhabited by a stock with a more conventional population structure, with a high proportion of young animals and a continuously decreasing number of older age groups. This reflects a population with constant and successful reproduction, recruitment and mortality. Variability of these parameters in the eastern region seems much lower than in the western sector or upstream of these areas.

4. Discussion and conclusions

4.1. Krill density

Average krill densities (38.3 krill per 1000 m^3 for the Scotia Sea to 754.3 krill per 1000 m^3 for the South Sandwich Islands region) were in the lower range of values estimated for 1985–2001 (7–637 krill per 1000 m^3) in the long-term Elephant Island mesoscale survey (Siegel et al., 2002). However, before 1985 density in the Elephant Island area was regularly above this level (188–1681 krill per 1000 m^3); thus, the present krill density for the Scotia Sea is still below the lowest value of the high-density period before 1985. The subareas around South Georgia (48.3) and the Antarctic Peninsula (48.1) had the lowest krill densities during the present survey, while these are thought to be predictably high-density areas for the krill fishery. The density results for South Georgia and the Antarctic Peninsula are similar to the low-density means for the krill-poor period of the 1990s. Contrasting with these observations are the high-density values from the South Sandwich Islands due to the high number of young, juvenile krill in that area. Unfortunately, no directly comparable data are available from other years for this area.

There are few other recent large-scale krill surveys for the Southern Ocean. The FIBEX Survey used different gear types (ranging from bongo nets to commercial trawls) such that direct comparisons of net sampling densities are not possible. Sushin and Shulgovsky (1999) reported krill biomass densities for the 1984, 1985 and 1988 summer seasons for an area similar to that of the CCAMLR 2000 Survey, but excluding the South Sandwich Island region (Table 7). Biomass varied little between years: 7.7–10.2 g m^{-2}. These data are best compared with those of Table 2 for the Scotia Sea and Antarctic Peninsula or for Subareas 48.1–48.3 (6.2–29.3 g m^{-2}). However, it should be noted that the depth range sampled in the surveys differed, with Sushin and Shulgovsky (1999) sampling the top 100 m in contrast to the upper 200 m of the CCAMLR 2000 Survey. As krill occur more frequently in the top 100 m, sampling restricted to this depth range may overestimate krill density relative to studies sampling over a greater depth range. Thus, the year 2000 estimates are probably slightly higher than the biomass densities reported by Sushin and Shulgovsky (1999).

Although biomass estimates for the Scotia Sea appear relatively stable over the three years studied by Sushin and Shulgovsky (1999), the density distributions showed substantial differences between years. While krill density showed some interannual fluctuation within all regions of the southwest Atlantic, these changes were moderate in the Antarctic Peninsula and South Orkney regions (47–176 g 1000 m^{-3} between years, Table 7) but dramatic off South Georgia (0.6–147 g 1000 m^{-3}). In 1985, krill were virtually absent from the South Georgia region while densities remained relatively high further south.

Such periodic large-scale changes in krill biomass across the region may be due to large-scale ocean–atmosphere processes. Priddle et al. (1988) described the effect of atmospheric influences on the density and distribution patterns of the krill stock(s) at South Georgia, whereby strong and persistent northerly winds displaced water masses to the south—thus disrupting the normal transport of krill into the South Georgia region. The high variability in occurrence and abundance of krill in the waters off South Georgia also may be due to these being at the extremes of the geographical range of *E. superba* rather than at the center of its distribution.

Another large-scale study was carried out in the Indian Ocean in summer 1996 (Nicol et al., 2000) in which krill density was much lower than reported here, i.e. 0.38 g m^{-2} versus 18.7 g m^{-2} (Tables 2 and 7). These Indian Ocean values are

Table 7
Krill numerical and biomass density derived from net and acoustic surveys in the Atlantic and Indian Ocean sectors of the Antarctic

Geographic region	Year	Net or acoustic	Mean biomass or numerical density			References
			$g\,m^{-2}$	$g\,1000\,m^{-3}$	$n\,1000\,m^{-3}$	
Southwest Atlantic	1981	Acoustic	8.0–64.4			Trathan et al. (1992)
Antarctic Peninsula		Acoustic	8.0–95.0			Lascara et al. (1999)
Antarctic Peninsula		Acoustic	8.0–138.0			Ichii et al. (1998)
Elephant Island	1990–97	Acoustic	9.6–100.4			Brierley et al. (1999)
S. Orkney Islands		Acoustic	17.1–26.3			Kasatkina et al. (1996)
S. Orkney Islands	1994	Acoustic	10.7			Brierley and Watkins (1996)
South Georgia	1990–97	Acoustic	1.87–94.9			Brierley et al. (1997)
Bellingshausen Sea	1993	Acoustic	19.6–42.6			Murray et al. (1995)
SW Indian Ocean	1981	Acoustic	2.3			Trathan et al. (1992)
W Indian Ocean	1996	Acoustic	5.54			Pauly et al. (2000)
Indian Ocean	1977–90	Acoustic	1.3–187.7			Pakhomov (1995, 2000)
Scotia Sea 30–60°W	1984	Net	7.7	76.5		Sushin and Shulgovsky (1999)
Scotia Sea 30–60°W	1984/85	Net	10.2	101.7		Sushin and Shulgovsky (1999)
Scotia Sea 30–60°W	1988	Net	10.1	101.4		Sushin and Shulgovsky (1999)
Antarctic Peninsula	1984–88	Net		47.6–176.0		Sushin and Shulgovsky (1999)
South Orkney Islands	1984–88	Net		70.8–130.5		Sushin and Shulgovsky (1999)
South Georgia	1984–88	Net		0.6–147.5		Sushin and Shulgovsky (1999)
Elephant Island	1978–01	Net	0.8–46.8	4.4–376.1	6.8–637.6	Siegel et al. (2002)
N Weddell Sea	1988/89	Net	0.03–2.06	0.5–34.3	0.9–62.4	Siegel and Harm (1996)
Bellingshausen Sea	1994	Net	0.03–0.30	0.15–1.52	0.2–2.7	Siegel and Harm (1996)
Indian Ocean 30–50°E	1984–89	Net	1.0–6.3	4.8–39.3	16.4–122.3	Pakhomov (2000)
Indian Ocean 60–80°E	1984–89	Net	0.5–8.9	3.1–58.7	3.3–139.9	Pakhomov (2000)
Indian Ocean 60–64°E	1984	Net	3.1	62		Aseev et al. (1988)
Indian Ocean 120–140°E	1984	Net		0.3–15.5		Terazaki and Wada (1986)
Indian Ocean 135–140°E	1996	Net			0.1–20	Chiba et al. (1998)
Indian Ocean 80–150°E	1996	Net	0.375		2.65	Nicol et al. (2000)
Indian Ocean 80–115°E	1996	Net	0.645		4.73	Nicol et al. (2000)
Indian Ocean SIBEX II	1985	Net	2.03		5.94	Hosie et al. (1988)
Ross Sea	2000	Net		9.3	10.9	Sala et al. (2002)

more than an order of magnitude lower than the Atlantic krill densities, especially if those areas thought to be located beyond the krill distribution range are excluded. Data from more restricted regional surveys also confirm that krill density is generally lower in the Indian Ocean than the southwest Atlantic (Chiba et al., 1998; Hosie et al., 1988). Although Pakhomov (2000) listed some high-density net estimates for the Indian Ocean (Table 7), these were mostly from the upper surface layer and are not directly comparable with those of the CCAMLR 2000 Survey. Samples that include the low-density depth strata have a relatively low krill density compared to those from the southwest Atlantic.

The same difference between Atlantic and Indian Ocean sectors can be seen from acoustic estimates. According to Pakhomov (2000), krill biomass density appears to have decreased after a peak in the 1970s, with low values persisting throughout the 1980s. Pauly et al. (2000) estimated an overall mean biomass density of $5.54\,g\,m^{-2}$ for the summer 1996 season in the Indian Ocean, while Hewitt et al. (2004) estimated $21.4\,g\,m^{-2}$ for the southwest Atlantic, which was in the lower range of values recorded from multi-year summer surveys in the Scotia Sea (Brierley et al., 1997, 1999; Ichii et al., 1998; see Table 7).

The distribution of krill and especially the concentration of krill aggregations is often related to local topography, with high krill abundance occurring in shelf break areas, around banks and ridges (Stein and Rakusa-Suszczewski, 1984; Witek et al., 1982), and in the lee side of islands (Makarov et al., 1970). However, the difference in total krill biomass between the Indian and Atlantic Oceans cannot be attributed to the Atlantic sector having more shelf areas with larger krill aggregations, because the shelf areas are relatively small and the oceanic waters of the Atlantic and Indian Oceans show the same differences. In comparison with the Scotia Sea, acoustic observations show much smaller swarm densities and swarm sizes, and larger inter-swarm distances for krill aggregations in the Indian Ocean (Miller et al., 1993). Krill density in the Indian Ocean is lower than in the Scotia Sea owing either to a lower overall biomass or to dispersion over a wider latitudinal range. The latter was used by Siegel and Harm (1996) to explain the lower krill density but wider geographical range of krill in the Bellingshausen Sea compared to the Antarctic Peninsula region, where krill aggregations are compressed into a narrow belt.

Part of the CCAMLR 2000 Survey area has been studied in a series of long-term mesoscale surveys around Elephant Island. The krill biomass in this small region of Subarea 48.1 has undergone substantial fluctuations in the past 20 years. The three Soviet surveys from the 1980s discussed previously fall into a period of clearly declining biomass densities in the Antarctic Peninsula region, from 26.7 g m^{-2} in 1984 to 2.6 g m^{-2} in 1988 (Siegel et al., 1998). For Subarea 48.1 the biomass density of the present survey (8 g m^{-2}) is closer to the lower end of these biomass indices from the Elephant Island time series. However, the strong variability in the Antarctic Peninsula area is not reflected in the Soviet large-scale surveys of the Scotia Sea. One explanation may be related to the size of area surveyed; a smaller area shows more variability if there are changes in krill distribution even if the overall biomass of the region remains constant. An alternative explanation could be the existence of two stocks in the Scotia Sea with alternating/opposing population dynamics. At the scale of the Scotia Sea a decline in one stock (possibly Bellingshausen/Peninsula) would be balanced by a simultaneous stronger influence of the second stock (possibly Weddell Sea) and vice versa. In this case, the overall biomass in the Scotia Sea would appear stable despite large variability in the source regions. The potential existence of two stocks was discussed by Mackintosh (1973) and Everson (1976), and the hypothesis was supported by Siegel et al. (1990) describing differences in demographic parameters as indicators of krill stocks of different origin.

4.2. Overall distribution

Fronts are thought to be the main oceanographic features in the Scotia Sea, which affect the distribution of krill. The Polar Front is conventionally considered to be the northern boundary for krill distribution. However, although the CCAMLR 2000 Survey area was entirely to the south of the Polar Front (Brandon et al., 2004) net samples indicate that, even to the north of South Georgia, krill densities had decreased to zero before the Polar Front was reached. This indicates that the effective boundary for krill is likely to be south of the Polar Front.

The other major fronts in the Scotia Sea are the Southern Antarctic Circumpolar Current Front (SACCF), the Southern Boundary of the Antarctic Circumpolar Current (SBACC) and the Weddell Scotia Confluence (WSC). Their locations during the CCAMLR 2000 Survey are reported by Brandon et al. (2004). The SACCF and the SBACC are close together in Drake Passage north of the South Shetlands (approximately 140 km apart), diverge slightly as they move northeastward into the Scotia Sea, and are then up to 700 km apart in the eastern Scotia Sea. These fronts are high energy features and are frequently associated with increased current speeds (Orsi et al., 1995). There is potential for these fronts to concentrate krill as increased local biomass or to separate different parts of the stock, e.g., separating feeding from spawning grounds or separating developmental stages. The fronts also may play a significant role in the transport of krill across the Scotia Sea. Fedoulov et al. (1996) suggested that the WSC may transport krill across the Scotia Sea, while the models of Hofmann et al. (1998)

emphasize the role the SACCF may play in the transport krill from the Antarctic Peninsula to South Georgia. The results of a model applied by Murphy et al. (2004) showed transport of krill from the Antarctic Peninsula to South Georgia, and also that a large proportion of the biomass may pass to the south of South Georgia and drift around the northern end of the South Sandwich Islands. Murphy et al. (2004) also showed that krill dispersion is not driven solely by the large-scale flow, but that biological phenomena—such as vertical migration (Godlewska, 1996)—also may be important.

In January/February 2000, the major krill concentrations occurred to the south of the SACCF (Fig. 3). However, around South Georgia where the SACCF deviates to the north, krill were observed to the north and west of the front. The highest krill densities occurred either side of the SBACC, especially in the meander close to the South Sandwich Islands. However, whether these krill concentrations are directly related to the frontal current is uncertain, because most of the concentrations occurred within 50–100 km of the front. The WSC, which ran from the eastern tip of the South Shetland Islands to the northeast of the South Orkney Islands and disappeared at around 35°W (Brandon et al., 2004), showed no relation to higher density areas in the western Scotia Sea.

The fronts did not separate the various krill size clusters (Fig. 5). East of South Georgia the SACCF crossed C1 (small krill) and C2 (intermediate length classes), and the SBACC dissected C1, C2 and C3 and even the sub-groups were not obviously related to either front. Gravid females occurred on both sides of the SBACC between Elephant Island and the South Orkney Islands (Fig. 10). The high-density area of gravid females in the eastern Scotia Sea was connected to the SBACC meander; however, in the central Scotia Sea there was no spawning stock associated with the front. Krill larvae (Fig. 11) seem to concentrate on both sides of the SBACC in the central Scotia Sea and had spread north across the two frontal systems, while gravid females only occurred to the south of the SACCF. The movement of krill larvae is more passive than for the motile adult developmental stages and this northward dispersion may be due to different vertical migration patterns. Murphy et al. (2004) show a more northerly component to krill trajectories modeled without including vertical migration.

There seems to be no general correlation between krill occurrence and the frontal systems of the Scotia Sea. It is likely that krill move freely across the various fronts and that fronts are neither aggregating krill nor segregating developmental stages. Surface water heats up in the summer and often creates a cap of fully mixed water over the underlying density structure. Krill live preferentially in this surface layer and could easily move from one side of the front to the other. The frontal zones also appear to have little effect on the distribution of other zooplankton (Ward et al., 2004). The same species assemblages were observed on both sides of the WSC, although the dominance and densities of certain species differed on either side of the front (Marin, 1987; Siegel et al., 1992).

4.3. *Krill spawning stock and larvae*

Length-frequency distributions and maturity stage composition showed substantial variation across the survey area. Gravid and spent females were not evenly distributed across the Scotia Sea. The distribution of the spawning stock showed two hot spots, the first along the outer shelf/open ocean region between the Antarctic Peninsula and the South Orkney Islands and the second around the central and southern South Sandwich Islands. A large discontinuity in the distribution of the spawning stock between 30° and 45°W in the central Scotia Sea and around South Georgia also was evident.

In those areas where gravid stages frequently occurred, immature developmental stages were often proportionately big in size (Fig. 6). This probably indicates that many of the immature krill in C3 (at least from their external sexual characteristics) were undergoing post-spawn regression. Regression and possible re-maturation of adult specimens after spawning was described in detail by Makarov (1975) and Poleck and Denys (1982). They found that several molts after spawning krill no longer show clear characteristics of spawning and that these specimens are difficult to distinguish from pre-spawning stages. This interpretation of post-spawn regression is supported by the high abundance of krill larvae in the central Scotia Sea during the survey period. It is thus possible that the number of spent animals might have been even higher than the number of females recorded as stage 3E might suggest. Many of the 'externally pre-spawning' stages (male 2A3) might in fact have already finished spawning and recovered from the process. This suggests that the spawning season had already passed its peak in early February.

Although Antarctic krill are thought to spawn between late November and April, the onset and duration of spawning shows interannual variability (Siegel and Loeb, 1995; Spiridonov, 1995). A maturity index of 0.79 (Loeb et al., 1997; Siegel and Loeb, 1995) suggests that the 1999/2000 spawning season had started very early. An early spawning event is supported by the abundance of surface larvae of calyptopis and furcilia stages in the RMT1 samples. Krill take round 85 days to develop to furcilia 3 stage and 30–45 days to calyptopis 1 or 2 (Ikeda, 1984). The first appearance of F3 was in the last week of January. This indicates that the first spawning occurred around 15 November. F1 stages were observed more frequently from 15 January onward, being about 63 days old. Their birthday would also be around 15 November. However, the majority of larvae were in calyptopis stage 1 or 2 with a maximum abundance between 20 and 30 January. The approximate timing of maximum spawning due to the dominant calyptopis stages would be around 20 December. This is similar to the 1981 FIBEX Survey, when at the end of January/beginning of February about 63% of the larvae were in calyptopis stage 1 and 25% in calyptopis stage 2. Working backward, Rakusa-Suszczewski (1984) concluded that in 1980/1981 the most intense spawning occurred in late December. According to Siegel and Loeb (1995) early spawning events are advantageous for a successful reproductive season and should produce a high spawning success and that ultimately leads to strong recruitment into the adult population. Sampling during the 2001 Elephant Island survey has confirmed the strength of the 1999/2000 year class, with the recruitment index ($R_1 = 0.57$) well above the long-term average (Siegel et al., 2002).

Quantitative large-scale larval surveys are scarce in the published literature. A survey of the Indian Ocean in 1996 recorded 2.5 larvae m^{-2} (adjusted from larvae 1000 m^{-3}) in the western sector and 637 larvae m^{-2} in the eastern sector (Nicol et al., 2000), although these differences between the eastern and western sectors are almost certainly due to survey timing. Brinton et al. (1986) cited average larval densities of 35 m^{-2} in the Scotia Sea during summer 1984, fewer than observed in 1981 (the FIBEX year) (Rakusa-Suszczewski, 1984; Brinton, 1985) but still substantial for the 1984 season. Therefore, krill larval concentrations of the magnitude observed during the CCAMLR 2000 Survey must be considered high. However, the 1981 spawning season was unusual in that krill larval densities were an order of magnitude higher than during 2000. The 1981 year class was the most successful since 1975, in terms of proportional as well as absolute recruitment.

During the FIBEX Survey the highest numbers of larvae were recorded in the central Scotia Sea, in the open ocean and along the shelf slopes (Rakusa-Suszczewski, 1984), as in the present survey. The areas around South Georgia and the South Sandwich Islands were not sampled during FIBEX, so it was not possible to see whether the sharp decline in larval density around 36°W and to the south of South Georgia also occurred during 1981. However, the Discovery data show a similar large-scale distribution of krill larvae; maps show a concentration of calyptopis and furcilia between 27°W (South Sandwich Islands) and 60°W (South Shetland Islands) for January to February (Fig. 100 in Marr, 1962).

Despite the short period between spawning and the occurrence of surface larvae, the distribution of larvae did not match the sharp decline in the main spawning stock in the western part of the Scotia Sea at 45°W. In contrast, the larvae (mainly calyptopis), which had undergone 30–53 days of development, had a more extensive range, having dispersed 240 miles farther north from around 59°–55°S and 250 miles farther east from 45° to 36°W. The sequence of larval occurrence over the summer and autumn reported by Marr (1962, Fig. 130) also shows the origin of the mass surface larvae to be the central to western Scotia Sea, with a subsequent eastward spread beyond the South Sandwich Islands. To the east of these islands larvae enter the 'Weddell Stream' (term by Marr, 1962), and which probably corresponds to the Antarctic Circumpolar Current, in particular to water to the south of the SACCF (see Brandon et al., 2004).

Numerous surveys around South Georgia have failed to identify spawning areas close to the island (Marr, 1962; Ward et al., 1990). Catches of larvae have been reported to the south and east of the island (Ward et al., 1990) in the 'Weddell Stream', and although krill eggs were found in January and March (up to 1000 m^{-2}) older larvae were absent (Witek et al., 1980). Variability around South Georgia seems greater than in the central Scotia Sea owing to its proximity to the northern limit of krill distribution and to the Polar Front. Oceanographic and atmospheric influences from beyond the Polar Front increase the complexity of dynamic processes in this region.

4.4. Population structure and recruitment

The length-frequency data indicate similarities in the krill stock composition across the southwest Atlantic, but with pronounced differences between subareas or larger geographical units. In most of the Scotia Sea/Antarctic Peninsula region, large krill were proportionately more abundant in the population. The modal size classes of 48 and 52 mm (4–5-year olds) krill represent the 1995 and 1996 year classes, which were the most successful year classes during the 1990s. Since then, recruitment has been poor at least in waters influenced by the outflow from the Drake Passage/Antarctic Peninsula region. However, there are signs from the spawning stock that krill recruitment was successful during the 2000 season.

The differences in length frequencies between the various parts of the Scotia Sea could suggest that each subarea was inhabited by different or independent krill stocks. Although Statistical subareas do not represent natural boundaries for the krill population, there are ecological units within the Scotia Sea which are important to krill demography and distribution. Figs. 4 and 5 for example show that small krill were distributed throughout a large proportion of Subareas 48.2 and 48.4. This size cluster formed a big intrusion and almost separated the western stock (C2a and C3 with mostly 4- and 5-year-old adults) from the eastern adult stock (C2b, C2c, C3 east with mostly 2-, 3-, 4- and 5-year-old krill). West of 45°W the stock was dominated by older krill, while the eastern section had a more complete set of age classes present. This 45°W boundary could be identified from krill demographic parameters such as recruitment and length-frequency distribution, as well as density and distribution of the spawning stock. In all, 36°W appears to be a boundary for the larval population originating from the South Shetland/South Orkney spawning event. However, discontinuities relating to behavioral phenomena are variable and move both throughout the season as well as from year to year, as is evident in the Discovery data (Marr, 1962).

Juveniles did not occur west of 45°W. This size class was well represented east of the South Orkney Islands in the Weddell outflow and extended north to the southern approaches of South Georgia. Murphy et al. (2004) used a modeling approach to trace the krill concentrations of the eastern Scotia Sea back in time. They predicted that krill found to the east of the South Orkney Islands in February 2000 were still under the pack ice of the northern Weddell Sea in late December 1999. The fastest retreat of the pack ice occurred over a two week period in late December/early January (Fig. 1), whereas stations between the Antarctic Peninsula and west of the South Orkney Islands were free of ice at the beginning of December. Sea surface temperature data (Naganobu, 2002, pers. comm.) also show the eastern Scotia Sea around 30°W to be influenced by the ice cover for a much longer period, identified by Brandon et al. (2004) as Weddell Sea water. These differences in the length and maturity composition of the sub-populations of krill in the Scotia Sea suggest the possibility of different origins for the krill aggregations. Large adults dominated the stock in Drake Passage water and extended east to the South Orkney Islands, intermediate-sized krill occurred to the south and separated the large-sized krill from the outflow of the Weddell Sea. Thus, the largest krill were linked to the area to the west of the Antarctic Peninsula and were probably of Bellingshausen Sea origin, while the juveniles in the eastern Scotia Sea around 30°W were from a source associated with a cold water intrusion from the Weddell Sea (Naganobu, 2002, pers. comm.).

Various regions of the Scotia Sea show similar composition of the krill stock. This may be due to similar physical forcing mechanisms affecting krill physiology over large areas. However, distributions of developmental stages and size groups extend beyond oceanographic fronts, with different oceanographic conditions either side of the fronts. Thus, it is likely that these regions are directly linked by the continuous flow of krill (e.g. C2), but also may be inhabited by krill from different sources, e.g., C1 and C2 sub-groups occurred in different parts of the Scotia Sea. This has implications for mesoscale surveys in CCAMLR Statistical subareas. At least in some years these mesoscale surveys may not adequately represent the composition and abundance of the krill populations in the southwest Atlantic. Conversely, in other years a high degree of similarity has been found between Subareas 48.1 and 48.3 (Brierley et al., 1999). Siegel and Harm (1996) have shown that the mesoscale surveys in the Elephant Island/Antarctic Peninsula areas represent the stock composition along the western side of the Antarctic Peninsula well into the Bellingshausen Sea. However, that the Atlantic Sector exhibits considerable interannual variability in the influence of the Antarctic Peninsula and Weddell Sea, causing differences for the two krill stocks in terms of abundance, age/size composition and recruitment success. This highly dynamic situation creates difficulties for the management of krill in the South Atlantic (Area 48) and argues for further large-scale krill surveys as well as a sub-division of the area into smaller management units.

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